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This is a pre print version of the following article:

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1728420> since 2020-02-19T09:23:18Z

Published version:

DOI:10.1016/j.scitotenv.2019.01.122

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Biodiversity of leaf litter fungi in streams along a latitudinal gradient

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Abstract

Global patterns of biodiversity have emerged for soil microorganisms and particularly for macroorganisms. The significance of microbial functions in ecosystems is also well established. Virtually unknown, however, are large-scale patterns of microbial diversity in freshwaters, despite the importance of these ecosystems as hotspots of biodiversity and biogeochemical processes. Here we report on the first large-scale study of biodiversity of leaf litter fungi in streams along a latitudinal gradient unravelled by Illumina sequencing. The study is based on fungal colonization experiments of standardised plant litter in 19 globally distributed stream locations between 69°N and 44°S. Fungal richness showed a hump-shaped distribution along the absolute latitude. Strikingly, community composition of fungi was more clearly grouped according to thermal preferences than to biogeography. Our results suggest that identifying differences in key environmental drivers, such as temperature, among taxa and ecosystem types is critical to developing an overarching theory of global diversity distribution of aquatic fungi.

Introduction

The role of freshwater ecosystems as components of the global carbon cycle is being increasingly acknowledged (Perkins et al. 2012; Martinez et al. 2014). Streams are hotspots of CO₂ emission (Perkins et al. 2012; Battin et al. 2009) as they receive organic carbon of terrestrial origin and its in-stream decomposition releases CO₂ to the atmosphere. The underlying processes, including the decomposition of terrestrial plant litter, are mainly driven by the activities of fungi (Boyero et al. 2011; Duarte et al. 2016b; Duarte et al. 2015; Seena et al. 2017). Importantly, decomposition rates of litter in streams can be affected by fungal diversity, either directly or through trophic effects (Jabiol et al. 2013b). Therefore, it is essential

to understand the global distribution and richness of aquatic fungi, to allow predictions of ecosystem responses to global changes (Violle et al. 2014).

There has been considerable debate as to whether microbes follow similar global distribution patterns as plants and animals (Fuhrman et al. 2008; Fierer et al. 2011; Azovsky and Mazei 2013; Tedersoo et al. 2014). Currently discussed topics include whether microbes follow a latitudinal diversity gradient characterized by increasing richness from the poles to the tropics (Hillebrand 2004; Mittelbach et al. 2007; Fuhrman et al. 2008; Andam et al. 2016) and to what extent biogeographic history structures present-day species distributions. The importance of plate tectonics as a significant factor governing the global distribution of plants and animals is well established (Holden 2012; Cox et al. 2016a; Briggs 1995), with many taxa following either the Laurasian or Gondwanan distribution patterns (Holden 2012). In contrast, one of the most enduring tenets in microbial ecology is Baas-Becking's hypothesis that "*everything is everywhere, but the environment selects*" (Baas-Becking 1934; O'Malley 2007), implying that latitudinal and biogeographical patterning of microbial diversity is weak or non-existent. Nonetheless, Taylor et al. (2006) concluded that microfungi do have a biogeography and that fungal species do not necessarily occur everywhere.

The richness of soil fungi (with some exceptions) generally decreases towards the poles (Tedersoo et al. 2014; Sul et al. 2013), with soil fungi that show strong dispersal abilities dominating at high latitudes (Cox et al. 2016b). Large-scale studies have also demonstrated that soil fungal richness is influenced by climate as well as by chemical and physical soil properties (Tedersoo et al. 2014; Zhou et al. 2016). Lastly, evidence exists for strong geographic structure and dispersal limitation of soil fungi (Talbot et al. 2014; Tedersoo et al. 2014). In a previous study, species richness of aquatic hyphomycetes, a polyphyletic group of stream fungi that assume dominant roles in litter decomposition, peaked at mid-latitudes and was lowest towards

the extremes of the latitudinal gradient on the northern hemisphere, with the exact shape of the diversity pattern modified by the chemistry of the litter examined (Jabiol et al. 2013a).. However, the study was based on only five streams and therefore of limited statistical power. A globally congruent pattern of stream microbial diversity has yet to emerge.

The objective of this study was to determine the community composition and diversity of litter-associated fungi, assessed as richness of operational taxonomic units (OTUs), in a coordinated global-scale study stretching over a 113° latitudinal gradient of 19 stream locations on five continents. Given that latitude is widely accepted as an overarching climate surrogate (Parmesan and Yohe 2003; Jetz et al. 2008; Boyero et al. 2011; Jabiol et al. 2013a), we tested the hypothesis that fungal richness decreases with latitude, similar to the pattern described for macroorganisms. Furthermore, we predicted that the global distribution of microbial taxa would follow the terrestrial biogeographic realms, eight of which are generally recognized to be based on distributional patterns of terrestrial species that result from isolation of populations by continental drift (Olson et al. 2001).

Materials and methods

Study sites and field work

A total of 19 study streams were distributed across both hemispheres with locations extending from 69° N to 44° S (Table 1 and Fig. 1). Mean annual air temperature (°C) and rainfall (mm) data were obtained from climate-data.org (<http://en.climate-data.org/>; accessed February 2016) and AIC (Autoridad Interjurisdiccional de Cuencas de los Ríos Limay, Neuquén y Negro, Bureau of Water Resources Management, Argentina; <http://www.aic.gov.ar/aic/default.aspx#v>; accessed February 2016). Characteristic properties of the experimental streams were: (1) low order (1-3 according to Strahler (Strahler 1957)); (2) <50 cm depth and <5 m wide; (3) coarse substrates, generally dominated by cobbles; (4) no

major anthropogenic impacts; and (5) no invasive tree species. Stream physico-chemical characteristics including concentrations of nutrients (nitrogen [N] and phosphorus [P]) were determined (APHA 1995) when the litter was deployed and retrieved.

Alnus glutinosa (L.) Gaertn. (black alder: Betulaceae) leaves were collected at a single site on the banks of the Mondego River at Lages, Coimbra (40°11'21"N, 8°25'30"W"). Black alder was chosen because the genus is widespread in the Holarctic and also occurs in the Neotropics (Boyero et al. 2011) and has high-quality leaves (Royer and Minshall 2001; Hladysz et al. 2009; Fernandes et al. 2014). Although alder trees do not occur in some of the study regions, their high-quality leaves (i.e., soft, high nitrogen concentrations) do not impose any colonization challenge to microbial communities (Fernandes et al. 2014; Royer and Minshall 2001; Hladysz et al. 2009; Chauvet et al. 2016). Moreover, the species has been previously used as a standard litter in global decomposition studies (Boyero et al. 2011), and the leaves are readily consumed by tropical detritivores (Encalada et al. 2010).

Kits containing air-dried alder leaves (three replicates, each containing 2 g of leaves), fine-mesh (0.5 mm) nylon bags, DNAgard® (Biomatrica, San Diego, CA, USA) and protocols were shipped from Coimbra, Portugal, to the other 18 locations distributed on all continents. DNA was extracted and pooled from 10 leaf discs (12 mm diameter) cut from randomly selected alder leaves and composition of the initial microbial community was determined by Illumina MiSeq sequencing before shipping. The leaves were not sterilized before colonization to avoid changes in litter chemistry (Howard and Frankland 1974). Microbes initially present on the litter have little influence on microbial colonization dynamics (Bärlocher and Kendrick 1974), since stream microbes are rapid colonizers that quickly outcompete terrestrial taxa (Nikolcheva et al. 2005; Frossard et al. 2013).

Strictly standardized litter colonization experiments were conducted in the 19 study streams during the dry season in tropical and during autumn in temperate and arctic streams. At each site, litter bags were deployed in riffle areas rich in oxygen (see Table S2) at water depths of less than 30 cm. Experiments were terminated when an estimated 40-50 % of the initial litter mass was lost, as inferred from previous decomposition studies (Boyero et al. 2011; Boyero et al. 2015). The exact colonization period at each site is given in Table S1. Three litter bags were retrieved and 10 leaf discs (12 mm diameter) were cut per bag with a sterile cork borer, immediately placed in 3 sterile screw-cap tubes containing 1 ml of DNAgard[®] solution and sent to the laboratory at the University of Coimbra, Portugal, for DNA extraction.

DNA extraction, Miseq sequencing and diversity analysis

From each replicate set of 10 leaf discs, microbial DNA was extracted with the PowerSoil[®] DNA isolation kit (MoBio laboratories, Carlsbad, CA, USA) according to the manufacturer's instructions. The concentration of extracted DNA (>20 ng/μl) was confirmed with a NanoDrop 2000c spectrophotometer (Wilmington, DE, USA) before storing the DNA at -20 °C. The DNA of all replicate samples from each country were pooled and sent to Research and Testing Laboratory (Lubbock, TX, USA; [www. researchandtesting.com](http://www.researchandtesting.com)) for Illumina MiSeq sequencing using ITS primer pairs for fungi (ITS3 F: 5'GCATCGATGAAGAACGCAGC 3' and ITS4R: 5'TCCTCCGCTTATTGATATGC3') (White et al. 1990).

Quality trimming was performed on the fastq using the SolexaQA++ dynamictrim utility (Cox et al. 2010) with a minimum threshold of 25 and if after quality trimming the length of the reads became less than 50 bp it was removed. The forward and reverse reads of our dataset was merged by using FLASH (Magoč and Salzberg 2011). Dereplication step was used to remove duplicated reads by using VSEARCH software (Rognes et al. 2016). Chimera was removed using Mothur (version 1.39.5; Schloss et al. 2009) using the unified system for DNA based

fungus species (UNITE) and international nucleotide sequence databases (INSDC) fungus ITS databases (version released on 28.06.2017) as reference (Koljalg et al. 2013). The clustering of the OTUs was achieved by using Swarm (version 2.2.2; Mahé et al. 2014) and the longest sequence from each OTU was selected as representatives of each OTU. The singletons were removed from the analyses and assignment of taxonomy was performed with a BLAST of the OTU representatives against UNITE+INSDC fungus ITS databases (version released on 28.06.2017, <https://unite.ut.ee>). The robust assignment to the fungus kingdom was made for the sequences with E-values $< e^{-50}$ and sequence similarity $> 75\%$. Moreover, query sequences with an E-value between e^{-08} and e^{-50} with sequence similarity $> 75\%$ were manually checked against the 100 best-matching sequences for accurate assignment (Li et al. 2016). Raw sequences from the alder leaves before exposure in the stream and after retrieval of the leaves were deposited in the National Center for Biotechnology Information (NCBI) database (Sequence Read Archives; SRA) under accession numbers SRP072752 and SRP100503, respectively.

Data analysis

Rarefaction curves showing the number of sequences versus the number of fungus OTUs in all locations were computed to check whether OTU richness was close to saturation. The control OTUs were removed from the OTUs of the samples and the rarefied fungus richness and relative abundances were calculated. All analyses were conducted in R (R Development Core Team, 2011), using vegan package (Oksanen et al. 2011). Barplots of the fungus phylum were generated using average OTU relative abundance.

We conducted linear regressions (Zuur et al. 2007) to assess the relationship between the physico-chemical characteristics of the stream and the locations with latitude. A quadratic term was added to the linear regression model to assess the relationship between OTU richness and

Latitude. All regressions were performed using (R Development Core Team 2011). All data were checked for normality and homoscedasticity; where necessary, a natural log transformation was applied to meet these assumptions. A Bray–Curtis similarity matrix (Bray and Curtis 1957) was calculated based on the log transformed relative abundance data. Influence Differences in fungal community structure were displayed using Canonical Analysis of Principal Coordinates (CAP; Anderson and Willis 2003) based on relative abundances of OTUs. Permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) tested for differences between sample clouds which were separated by two CAP axes. Unrestricted permutation of the raw data at 9999 permutations was used for PERMANOVA. PRIMER 6 was used to perform PERMANOVA and CAP analyses (Version 6, Primer-E Ltd, Plymouth, UK; Clarke and Gorley 2006) A Venn diagram was generated with Venny 2.1 (Oliveros 2015) to determine the shared OTUs between the sample clouds which were separated by two CAP axes.

Results

Physico-chemical characteristics of streams

Mean stream water temperature during the study (3.1–26.2 °C), mean annual air temperature (0.9–27.4 °C), and mean annual rainfall (527–4273 mm) at the 19 locations of our study (Table 2) were all significantly related to absolute latitude (Fig. 2). The site in Ecuador appears to contradict this trend, however, it was located at an unusually high altitude (3061 m asl). There were no latitudinal trends in mean pH, conductivity or concentrations of dissolved oxygen, phosphate or nitrate.

Diversity of litter-associated fungi

Illumina MiSeq sequencing of colonized alder leaves revealed 1,093,416 reads. These were reduced to 859,892 after filtering for quality and length after joining the forward and reverse

reads it generated in total 229,194 reads. After dereplication this was further reduced to 44138 reads; after performing the chimera 42,618 reads remained (Table S2). The no hits and OTUs belonging to the kingdom Plantae (14.6%) were removed. The removal of the control OTUs from the samples yielded 1311 OTUs (Table S3). Collectively, fungal OTUs were assigned primarily to the phylum Ascomycota (79.71 %), followed by Mucoromycota (16.8 %), Basidiomycota (0.43%) and Chytridiomycota (0.2%). The remaining 10.62 % of the fungal OTUs were unknown. The relative abundances of fungal classes varied among locations: streams with water temperature (Fig. 3) above 8.6°C (except in Japan) consisted mainly filamentous fungi of moulds (Azores, Brazil, Canada, Ecuador, Hong Kong, Malaysia, Portugal, Spain and USA), Yeasts (India and Guinea) and unknown fungi and chytrids (Australia).

Fungal richness

Rarefaction curves of the streams had clearly distinct and separate trajectories, suggesting that they realistically represented inherent diversity patterns (Fig. S1). OTU richness was lowest at latitudinal extremes, peaked at mid-latitude regions (Fig. 4), and was insensitive to major climatic factors like temperature or rainfall.

Endemism and ubiquity

A total of 950 OTUs (out of 1311 OTUs) were unique to single locations and classified as exclusive endemics. The richness of endemic fungal species did not follow any specific geographical trend (Fig. S2). India and Hong Kong (97 %) had the highest fungal endemism, closely followed by Malaysia (72%), Portugal (55%) and Japan (54%). Australia and Guinea did not have any exclusive endemics. 93% of the total OTUs were restricted to two localities, showing moderate endemism. The majority of endemic fungi were in the Neotropic realm (55%) followed by Indo-Malay realm (40 %), the Palearctic (35 %), Australasia (21%) and

Nearctic realm (19 %). In our study, the Afrotropic realm did not have endemic fungi. Out of all fungi, 14.5% were aquatic hyphomycetes (litter decomposers), however, in France (48%), Germany (47.5) and Italy (46.8%) almost half of the fungi were aquatic hyphomycetes. The aquatic hyphomycete, *Lemonniera aquatica* was the most widespread species and occurred in 8 locations.

Influence of water temperature

To discriminate among drivers of community structure, canonical analysis of principal coordinates (CAP) using Bray–Curtis similarities from log-transformed relative species abundance data of OTUs was used. The resulting pattern was clear and the communities were separated into three groups ($\leq 8.1^{\circ}\text{C}$, $8.6\text{--}19.8^{\circ}\text{C}$ and $\geq 21.3^{\circ}\text{C}$) based on stream temperature, except for Japan (Fig. 5). The overall classification accuracy rate based on $\leq 8.1^{\circ}\text{C}$, $8.6\text{--}19.8^{\circ}\text{C}$ and $\geq 21.3^{\circ}\text{C}$ is 83.3 %, 87.5% and 80% respectively. The results demonstrated that the first ($\delta^2=0.9371$) and the second ($\delta^2=0.7978$) squared canonical correlation was large. The first canonical axis separated the communities of the tropical streams from others and the second axis separated the communities from the stream with the $8.6\text{--}19.8^{\circ}\text{C}$ temperature range to the others. A permutational multivariate analysis of variance (PERMANOVA) test demonstrated a significant effect of the stream temperature ($F_{2,18} = 2.19$, $P = 0.0001$). 773, 318 and 350 OTUs exclusively belonged to $\leq 8.1^{\circ}\text{C}$, $8.6\text{--}19.8^{\circ}\text{C}$ and $\geq 21.3^{\circ}\text{C}$, respectively. Streams with water temperature $\leq 8.1^{\circ}\text{C}$ and $8.6\text{--}19.8^{\circ}\text{C}$ shared 63 OTUs while streams with $\leq 8.1^{\circ}\text{C}$ and $\geq 21.3^{\circ}\text{C}$, and $8.6\text{--}19.8^{\circ}\text{C}$ and $\geq 21.3^{\circ}\text{C}$ water temperature shared 57 and 21 OTUs respectively (Fig. 6).

Discussion

One of the most studied and widely documented macroecological pattern is the latitudinal gradient in species richness. A decrease in species richness with latitude is the oldest and most

fundamental pattern of the distribution of life on earth, particularly in plants and animals (Peay et al 2016). As many factors (such as temperature, rainfall) change with latitude it is important to determine if litter associated fungi correspond to macroecological patterns, in order to recognize the general drivers of fungal biodiversity. A key discovery of our large-scale coordinated study is that the fungal richness diverges from the conventional macroecological pattern. In our study, it follows a hump-shaped relationship with absolute latitude with a peak at mid-latitude regions (temperate streams) (Fig. 4). This could be possibly due to more varied niches owing to the strong seasonality in the temperate streams (Shearer et al., 2007; Jabiol et al). In our study, stream temperature, air temperature and rainfall decreased with latitude, implying that extreme conditions were not favorable for litter associated fungi. A hump-shaped curve along the latitudinal gradient was also described in previous studies pertaining to aquatic hyphomycetes, the major litter decomposers (Jabiol et al. 2013a; Wood-Eggenschwiler and Bärlocher 1983; Shearer et al. 2007). This discrepancy differs strikingly from the global soil fungal study which demonstrated macroecological patterns similar to those of other organisms, albeit with several notable exceptions.

Stream and soil environments and their microbial communities differ in many fundamental ways (Vinson and Hawkins 2003, Bärlocher and Boddy 2016), implying that global microbial diversity patterns need not necessarily match. For instance, precipitation events affect fungal species richness in streams through hydrological disturbances such as droughts and floods, whereas the main control in terrestrial ecosystems is primary productivity (Hawkins and Diniz-Filho 2004; Hawkins et al. 2003). Similarly, moisture is a limiting factor in soils but not in (permanent) streams.

Our study demonstrates the tendency of litter associated fungi to occur in thermal bands. We identified three fungal clusters encompassing locations from different biogeographic realms.

These clusters corresponded to different stream water temperature bands, indicating that water temperature plays an essential role in determining the occurrence and composition of litter-associated microbes in streams across the globe. Given that aquatic fungi play a key role in litter decomposition in streams (Baldy et al. 1995; Weyers and Suberkropp 1996), and species differ in their preferred thermal ranges for growth (Krauss et al. 2011), reproduction (Chauvet and Suberkropp 1998) and activity (Ferreira and Chauvet 2011), large-scale variation and changes in temperature are likely to influence not only the composition of fungal communities (i.e. biodiversity patterns) but also rates of carbon and nutrient cycling (Martinez et al. 2014; Dang et al. 2009).

Our results show that even the most common fungi, *Lemonniera aquatica* was limited to 8 locations. Thus, freshwater fungi associated with decomposing litter appear to follow the 'moderate endemism model' of microbial biogeography initially proposed for small eukaryotes (Foissner 1999). However, this conclusion needs further backing by empirical data on a wide range of substrate and habitats before generalisations about global distribution patterns can be confidently made. This includes comparisons of different locations under similar climates and/or at similar latitudes to substantiate whether community similarity across regions is typically temperature-driven, as our results suggest.

Some published evidence indicates that the biogeography of freshwater fungi classified as aquatic hyphomycetes is species-specific (Duarte et al. 2012), and that, as confirmed here, community composition in geographically distant locations within comparable climatic zones may be similar (for review, see Duarte et al. 2016a). A caveat to generalisations about biogeographic patterns in microbial diversity is the fact that fungi undergo distinct successions during litter decomposition (Suberkropp 1984; Gessner et al. 1993).

The fungal communities in our globally distributed study streams were invariably dominated by Ascomycota as has been observed in soils (Schneider et al. 2012). In particular, fast-growing moulds like *Penicillium* and *Mucor*, yeasts, Chytrids were the most abundant fungi in streams with water temperature ≥ 8.6 °C (Fig. 3). The one exception is the stream in Japan, located at a higher altitude (1076 m) than the other locations (75 m - 300 m) within the same water temperature range (Table 1). Altitude is also known to play a significant role in structuring fungal communities in streams (Chauvet 1991), sediments (Wu et al. 2013) and soils (Siles et al. 2017).

Conclusions

Our results point to an overwhelming influence of temperature on the global distribution of litter-associated fungi in streams. This suggests that global warming might induce shifts in microbial communities colonizing decomposing litter in streams, particularly in communities with species adapted to cool environments (Christiansen et al. 2017) or those that currently experience minimal temperature fluctuations, such as in streams near the equator (Perez et al. 2016). A corollary of such community shifts that may involve the loss of key species is that expression patterns of enzymes essential in litter decomposition may lead to cascading adverse effects on food webs, alter biogeochemical cycles (Christiansen et al. 2017) and compromise ecosystem services and human well-being (Chapin et al. 2000; Sandifer et al. 2015; Wall et al. 2015).

Figure Legends

Figure 1: Study streams distribution across the globe. Norway (NOR), Germany (DEU), Canada (CAN), Italy (ITA), France (FRA), Spain (ESP), Portugal (PRT), United States of America (USA), Azores (AZO), Japan (JPN), Hong Kong (HKN), India (IND), Guinea (GIN)

Malaysia (MYS), Ecuador (ECU), Brazil (BRA), Australia (AUS), Argentina (ARG), New Zealand (NZL).

Figure 2: Linear regression model (n=19) of the relationships between absolute latitude and the natural logarithm of the mean annual rainfall (a), mean stream water temperature (b) and mean annual air temperature (c).

Figure 3: Relative abundance of fungal operational taxonomic units. For locations of stream sites see Fig. 1.

Figure 4: Polynomial regression model between absolute latitude and fungal OTU richness.

Figure 5: Canonical analysis of principal coordinates (CAP) ordinations of the relative abundances of fungal OTUs. Locations are colour coded according to mean water temperature. Mean water temperature bands were ≤ 8.1 , 8.6-19.8 and ≥ 21.3 °C. For locations of stream sites see Fig. 1.

Figure 6: Venn diagram showing the unique and shared OTUs between the stream water temperature groups. Mean water temperature bands were ≤ 8.1 , 8.6-19.8 and ≥ 21.3 °C.

Supplementary Figures

Figure S1: Rarefaction curves of fungal samples in all the streams across the globe.

Figure S2: Percentage of endemic species in the 19 streams across the globe. For locations of stream sites see Fig. 1

Acknowledgements

We are grateful to the Ecuadorian Ministry of Environment (Permits: #56-IC-FAU/FLO-DPN/MA, MAE-DNB-CM-2015-0017), and the village of Oyacachi for access to sites. Thank you also to A. Eguiguren and J. Martinez (Ecuador), S. Lamothe (France), M. Degebrodt (Germany), L.C.Y. Ng (Hong Kong) and C. Wahl (USA) for assistance in the field. Finally, we thank I. Abrantes for providing laboratory facilities.

Funding

This research was supported by the European Regional Development Fund-Operational Competitiveness Programme (FEDER-POFC- COMPETE; FCOMP-01-0124-FEDER-027793) and by national funds of the Portuguese Foundation for Science and Technology (FCT) through the project ‘DiverseAquaFun-Molecular profiling of taxonomic, functional and genetic diversity of aquatic fungi along a pollution gradient’ (PTDC/AAG-GLO/3896/2012) granted to S. Seena, PEst-OE/BIA/ UI4050/2014 granted to CBMA, and UID/MAR/04292/2013 granted to MARE. FCT also supported S. Seena and O. Sobral (PTDC/AAG-GLO/3896/2012), S. Seena (SFRH/BPD/103865/2014) and V. Ferreira (IF/00129/2014). The fieldwork performed in the Azores was funded by FCT (EXPL/AAG-GLO/0189/2013). The fieldwork conducted in Ecuador was supported by the projects DEB-1046408, DEB-1045960, and DEB-1045991. The funding bodies did not influence the design of the study and collection, analysis, and interpretation of data and in writing the manuscript.

Conflict of interest

The authors declare that they have no conflict of interest, financial or others.

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